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Studies in etiolation

AUGUSTINE DAWSON SELBY

(WITH PLATES 4 AND 5)

During the winter of 1902–1903 the writer carried on certain studies of the effects of etiolation upon several species of plants in the laboratories of the New York Botanical Garden. Most of the species studied were latex-bearing sorts. Owing to the press of regular duties, and to ill health, the publication of the results has been long delayed — far too long, indeed. It seems, however, worth while to present them briefly at this time. An announcement of the results obtained with *Persea* was made before the Botanical Society of America at its Washington meeting, January 1, 1903.

Seedlings of the Alligator pear (*Persea gratissima*) were grown in a dark room and propagating houses of the Garden, toward the end of 1902. At the end of ten weeks the normal and etiolated plantlets had developed stems approximately equal in length (about 45 centimeters) which consisted of 17 and 19 internodes respectively (plate 4, figure 7). The variation in the length of the internodes of the normal plantlets was slightly greater than with the etiolated. No acceleration was shown in rate of growth by the etiolated plants, nor was the total amount of growth greater than in the normal. The stem-diameters were nearly the same in both cases. All the leaves of the etiolated stems were bract-like and rudimentary (plate 4, figures 3 and 4); these did not advance beyond a certain stage of 10 mm. in length, with blades 5 x 2 mm., when they withered and dropped off. These rudiments seem generally comparable with the rudimentary organs borne on the basal

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portions of the normal stems. At the end of the period of growth studied, four weeks later, the thick cotyledons of the normal specimens were very much shrunken, discolored and decaying, while those of the etiolated plants were bright, plump, and yet retained reserve material. The contrast in this depletion of stored food was quite clear. An examination of the roots was made at the end of fourteen weeks and the total length of the roots of the etiolated plants was found to be about half that of the normal. The crowded and entangled growth of the roots of the normal plant was in marked contrast to that of the etiolated. A number of buds on the basal portion of the etiolated stems, including those axillary to the cotyledons, started into activity, but those of the normal stem remained dormant.

The cross-section of the middle portion of the normal stem (plate 4, figure 1) showed a fairly well developed woody cylinder about 300 μ thick, with definite cambium and numerous vessels in the wood. The bast-bundles were 48 in number, composed of lignified cells with laminae 3.5–4 μ thick, interspersed at times with unlignified, thin-walled cells; occasionally these latter contained chloroplasts. Usually the secondary bast-bundles were fairly well developed. The remaining cortex consisted throughout of thin-walled cells with a layer of more highly colored cells just without the bast, the whole covered by the unmodified epidermal cells. The cells of the pith frequently contained starch and the perimedullary ring was gorged with starch, as were also the medullary rays. The region of highly colored chloroplasts constituted also a well-marked starch ring at the base of the normal stem.

The cross-section of the etiolated stem (plate 4, figure 2) showed a woody cylinder 150–250 μ thick, consisting of slightly lignified cells, with less conspicuous cambium and with fewer and slightly smaller vessels in the wood. The bast consisted of the same number of bundles but with very slight development of the secondary bundles; the walls were thinner than in the normal and less lignified. The cortex contained fewer chloroplasts than the normal, while the two outer layers of the epidermal system were more or less collapsed and were underlaid by a well-marked hypodermal phellogen. The pith-cells of the etiolated stem were

larger than in the normal, while the same gorging of the stems with starch grains was noted in the perimedullary region and in the medullary rays. The earlier formation of phellogen in the etiolated stem may be interpreted as an adaptation to prevent drying out; this phellogen was present near the summit of the etiolated stem. This precocious phellogen formation, in this case with the early collapse of the epidermis, is similar to that observed by MacDougal in *Acer* and *Cornus*.*

Etiolated specimens with stems 50 to 60 cm. in length were brought into diffuse illumination near a window and in two months made an additional elongation of about 5 cm. The terminal newly formed portions of such stems bore about 7 normal leaves, with 8 or 10 internodes immediately below still retaining the bract-like organs resulting from etiolation (plate 4, figure 5). The lower portion of the stem, in which precocious development of phellogen had taken place, retained its brown color but was not extended, while the entire upper portion of the stem had become green. Young stems which had made but little growth in darkness made much more rapid growth than that described above for the older stems, and developed an equal crown of normal leaves.

The leaves of the normal plant (plate 4, figure 6) showed a single layer of palisade-cells and no stomata on the upper surface, as before noted by Solereder.† The petioles showed definite cambium, but the vessels gave no lignin reaction. The bract-like hairy leaves of the etiolated plant (plate 4, figures 3 and 4) showed no cambium in petioles, no stomata and no further differentiation of the tissues than an indistinct row of palisade cells, whose length and width were nearly equal.

Rootstocks of *Euphorbia corollata* obtained from Ohio, were also grown in light and darkness under conditions similar to those for *Persea*. No essential difference in the rate of growth, or in the total amount of tissue produced, was observed as between the normal and the etiolated growths of *Euphorbia* (figures *A* and *B*). There was noticeable variation in the thickening of the etiolated stems due to an increase of cortex by activity of the cambium layer.

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* MACDOUGAL, D. T. The influence of light and darkness upon growth and development (Mem. N. Y. Bot. Gard. 2:) 97–100, 188–190. 1903.

† SOLEREDER, H. Systematische Pflanzenanatomie 774. 1900.

The determination of the water and dry matter in the stems of these specimens gave the following results:

DRY SUBSTANCE IN STEMS OF *Euphorbia corollata*

	Normal plant per cent.	Etiolated plant per cent. I	II	Average.
Water	86.90	91.11	89.63	90.37
Dry substance	13.10	8.89	10.37	9.63

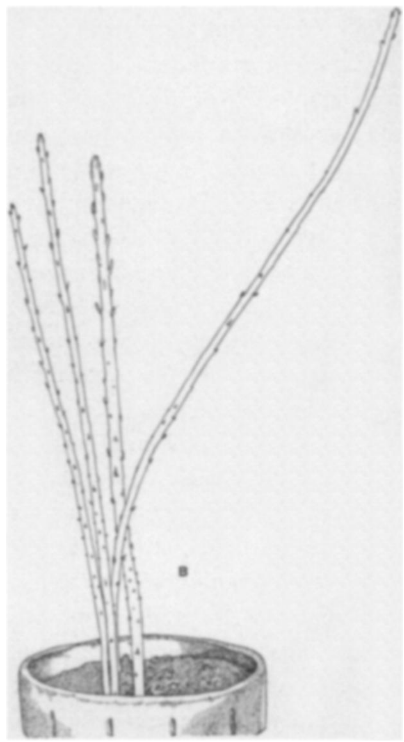


FIGURE A. Normal plant of *Euphorbia corollata*.
FIGURE B. Etiolated plant of *Euphorbia corollata*.

A transverse section of the stems showed (plate 5, figure 1) in the normal a rather feeble development of the strengthening tissue and a cambium of several layers of short cells. The woody parts of the cylinder were irregularly and feebly developed, bringing the groups of vessels into great prominence. The etiolated stem, as before stated, showed (plate 5, figure 2) a tendency to develop cortical parenchyma and the woody portion scarcely less devel-

oped than in the normal. These differences will be evident in the illustrations (plate 5, figures 1 and 2). Referring to the analysis it is observed that the increase in the thickness of the etiolated stems has not been accompanied by any considerable increase of solid matter and that the etiolated plant contains about 3½ per cent. more water than the normal. These results are in harmony with those previously obtained by others.

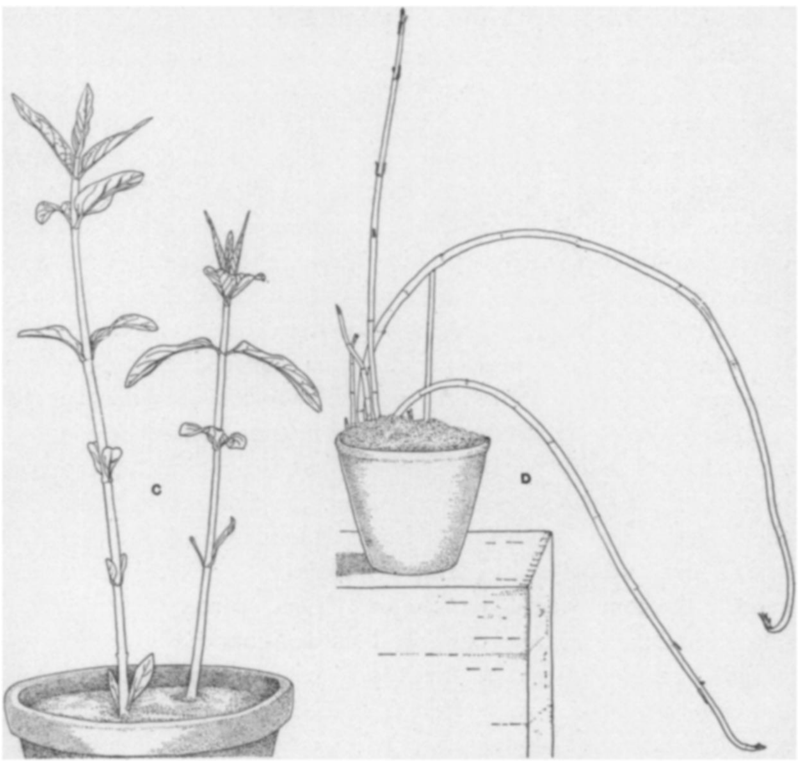


FIGURE C. Normal plant of *Asclepias incarnata*.
FIGURE D. Etiolated plant of *Asclepias incarnata*.

Roots of *Asclepias incarnata* were likewise collected at Wooster, and plants grown from them in the etiolating chamber and the propagating house of the New York Botanical Garden. The etiolated plants of this milkweed started to grow earlier than the normal, and produced longer stems (figures *C* and *D*). These developed as many as 13 or 14 internodes, with a length varying between 5 and 12 cm. The lower axillary buds of the etiolated

plants showed a tendency to start into activity during the growth of the main stem. The leaves were dropped from the etiolated stems, so that when the examination was made none were found below the tenth or twelfth internodes from the base; although in a few instances bract-like organs formed on lower internodes were retained for a long time. Normal stems of the same age produced but 7 to 9 internodes with an average length of 3–4 cm. It would appear from these facts that the abnormal length of the etiolated stems of this plant is due both to the exaggerated growth of the internodes and to the actual multiplication of the internodes.

The anatomical features present some interesting comparisons which may be studied by reference to the figures. In the etiolated stems (plate 5, figure 6) the cambium included four or five layers, while the woody cylinder and the bast-cells were less strongly developed than in the normal, as might have been expected. In the middle of the normal stem it was noted that the bast-sheath was more nearly continuous than at the base; a like condition, though less strongly marked, was also observed in the middle of the etiolated stem. In one instance an etiolated stem had become nearly prostrate by its own weight, and the apical portion had responded by an apogeotropic curvature which brought the tip into an erect position. Little difference could be detected in the structure of the central cylinder of these stems with respect to the convex sides, but the bast-fibers, scarcely differentiated on the convex side, were developed as well-marked strands composed of colums of two or three dozen cells in cross-section upon the opposite or concave side. This seems to show that while stretching tension might induce the development and differentiation of this tissue, the absence of stress, or positive compression resulted in the non-differentiation. Similar effects have been noted in special investigations, by various workers, dealing with the effect of compression and tension upon the mechanical tissues. Determinations of water were made in the normal and etiolated stems of this plant with the following results:

DRY SUBSTANCE IN PLANTS OF *Asclepias incarnata*

	Normal plant per cent.	Etiolated plant per cent. I	II	Average.
Water	86.58	91.83	91.57	91.70
Dry substance	13.42	8.17	8.43	8.30

Here we have wider divergence amounting to more than 5 per cent. difference in the dry substance of the normal above that of the etiolated stems.

Rootstocks of *Euphorbia Cyparissias* were brought from Wooster, Ohio, to the New York Botanical Garden, and after these had shown signs of activity were placed in suitable pots and some exposed to light while others were placed in the etiolating chamber, on March 20, 1903. The new stems were one to two cm. in height although none had formed chlorophyl to any noticeable extent. One month later the stem-lengths of the normal and etiolated plants were respectively 8 to 10 cm. for the normal and 6 to 8 cm. for the etiolated. It is evident that this plant does not support the assumption that light exercises an actual retarding effect upon growth.

Roots of *Apocynum cannabinum* were lifted and potted in November, 1902, and at this time duplicate pots were placed in the dark chamber and in the propagating house of the Garden; a large number of duplicates were cared for in the propagating house. The plants showed little tendency to make early growth in either situation. Toward the end of April, 1903, shoots began to appear on the plants in the dark chamber and a corresponding plant was set aside in the propagating house. In June, 1903, measurements were kindly taken by Dr. W. A. Cannon, laboratory assistant at the New York Botanical Garden. The etiolated plants attained a height of about 30 cm., while the normal specimens made no marked growth after having been set aside in April.

Similar results to those of *Apocynum* were obtained with roots of *Asclepias syriaca*. In this case the etiolated specimen attained a height of 30 cm. while the normal plant attained a length of but 5 to 6 cm., development being arrested for some reason.

Interpretation of results

It is evident from the foregoing that the phenomena of etiolation are not in themselves to be regarded as of a useful adaptive character, as put forward by many writers on the subject. In some instances it is conceivable that the undue elongation of stems that ensues might serve the useful purpose of carrying the apical part of the stem with its leaves past an obstruction intercepting the light, but a census of the species which have been sub-

jected to etiolation by MacDougal and others shows that less than half exhibit such elongations.

An important correlation-reaction is shown by the basal buds of etiolated stems. Numbers of such buds usually dormant are awaked in darkness and develop stems.

None of the facts derived from the study of the behavior of etiolated plants may be construed to indicate that light exercises a retarding effect on growth, however. If such a conclusion is to be maintained it must be justified on other grounds beside the results of studies of the action of plants in darkness.

A consideration of the structure of the plants studied in the work described above leads to the conclusion that when grown in darkness the tissues do not attain full development and that the differentiations by which the separate tissues are distinguished appear to be carried out only partially or not at all. The degree of incompleteness depends to some extent upon the organographic relations of the structures taken into consideration. This failure in the perfection of the tissues, which may even include their non-appearance, is very naturally coupled with a prolonged growth of the meristematic cells which by repeated division may thus increase either the thickness or the length of a stem.

Directly and indirectly, light seems to exert a stimulative effect upon the morphogenic processes leading to the differentiation of the tissues. If an etiolated shoot is brought into illumination, the portions in which the embryonic tissue has not gone beyond a certain age carry on development approximating the normal. Older etiolated tissues may form chlorophyl or undergo additional thickening of the walls, but no other differentiations in form are possible.

The formation of prosenchymatous cells in the concave side of a geotropically curving stem of *Asclepias*, in which they were lacking from the opposite convex side, is an excellent example of pure mechanical induction. In normal stems the development must set up, through the tension of the various tissues of the stem, stimuli which would induce the formation of prosenchyma regardless of the action of light. Now in the etiolated stem the bast-strands seem to be induced only by the bending strains exerted on the stems by their tendency to fall over, and the stresses

throughout the stem are otherwise equal, being simply those arising from turgidity. When such a stem is laid in a prostrate position and the embryonic cells of the apical portions of the stem produce a curvature in making an adjusting response, the stretching tension set up in the concave side of the stem acts as a stimulus inducing the formation of the mechanical tissue as described.

The writer wishes to express his great obligations to Dr. D. T. MacDougal, Director of the Laboratories of the Garden, for material aid and constant encouragement in the course of this work, and to make further acknowledgment of special assistance in the interpretation of results. The illustrations are chiefly from drawings made by A. Mariolle, of the Garden, to whom his best thanks are due.

OHIO AGRICULTURAL EXPERIMENT STATION.

Explanation of plates 4 and 5

PLATE 4

Persea gratissima

FIG. 1. Portion of cross-section of middle of stem of normal plant.

FIG. 2. Portion of cross-section of middle of stem of etiolated plant.

FIGS. 3, 4. Bract-like hairy leaves of etiolated plant, × 4½.

FIG. 5. Etiolated 10-weeks' seedling (same as figure 7), after two months' illumination, about one-fifth natural size.

FIG. 6. Leaf of normal plant, about one-half natural size.

FIG. 7. Etiolated 10-weeks' seedling, about one-fifth natural size.

PLATE 5

Euphorbia corollata

FIG. 1. Portion of cross-section of stem of normal plant.

FIG. 2. Portion of cross-section of stem of etiolated plant.

FIG. 3. Leaf of normal plant, two thirds natural size.

FIGS. 4, 5. Leaves of etiolated plant, × 1⅓.

Asclepias incarnata

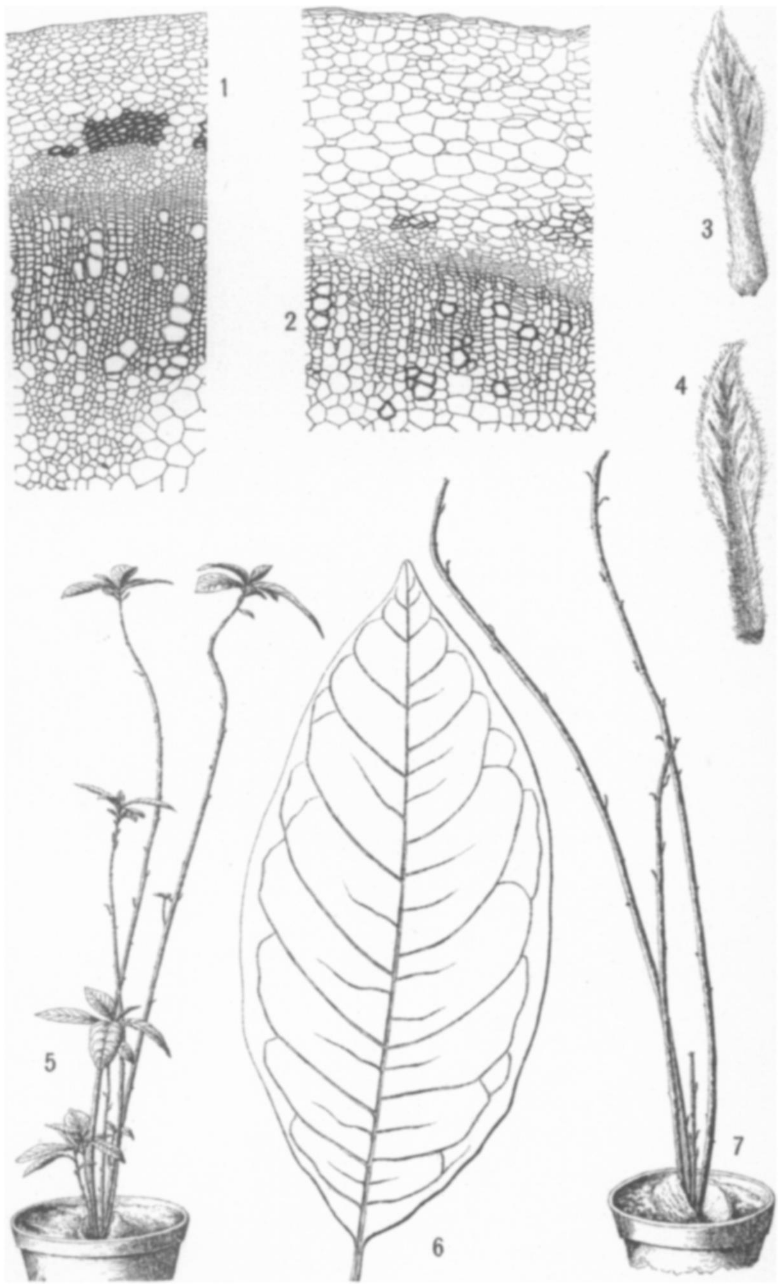
FIG. 6. Portion of cross-section of middle of stem of etiolated plant.

FIG. 7. Portion of cross-section of middle of stem of normal plant.

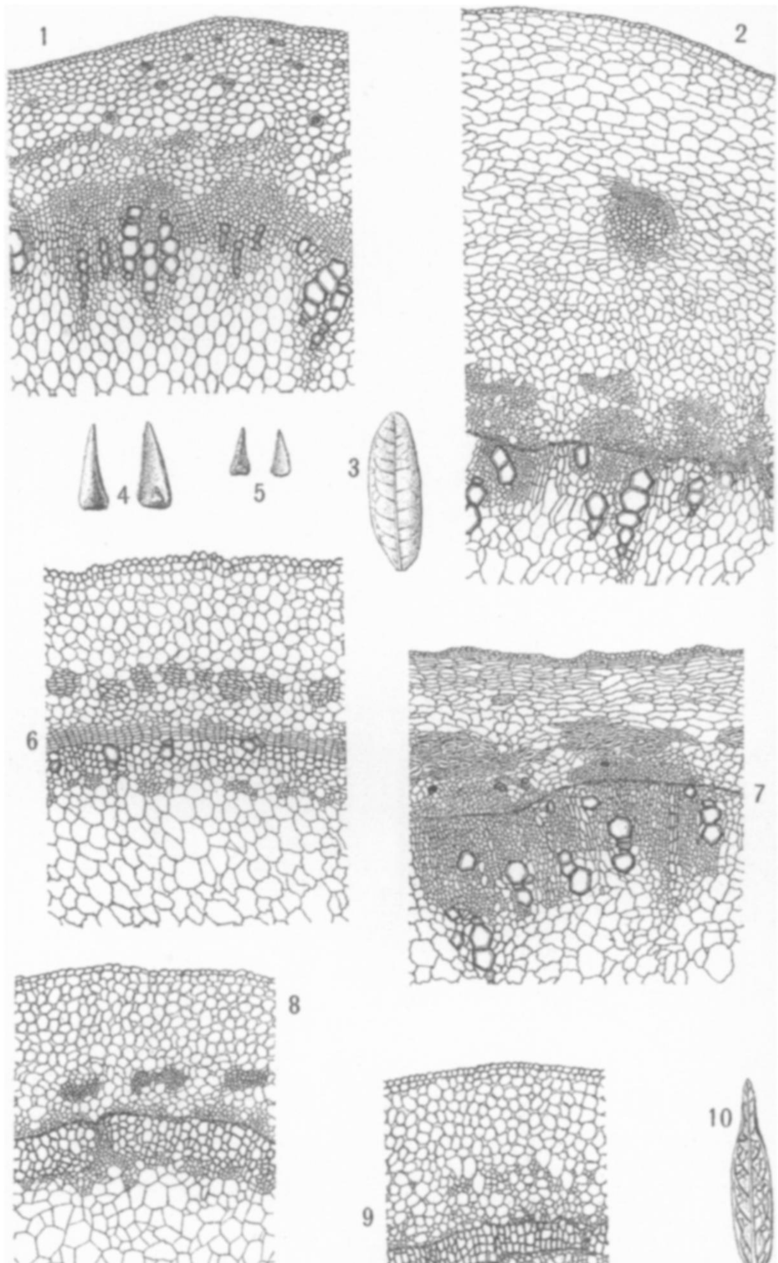
FIG. 8. Portion of cross-section of concave side of curved stem of etiolated plant.

FIG. 9. Portion of cross-section of convex side of curved stem of etiolated plant.

FIG. 10. Leaf of etiolated plant, × 1⅓.



STUDIES IN ETIOLATION



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